

TIME BUDGETS OF WYOMING GROUND SQUIRRELS, *SPERMOPHILUS ELEGANS*

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ABSTRACT.— Time budget of free-living adult *Spermophilus elegans* differed significantly from that of juveniles in the Front Range of the Rockies during 1974–1975. No differences were found between males and females. Hour of day, day since emergence, air temperature, cloud cover, and presence of predators all correlated with the frequency of various components of the time budget.

Study of time budgets is important in comprehending the roles of animals in ecosystems as well as understanding their basic patterns of behavior. Time budgets constructed for a few ground squirrels [the Columbian ground squirrel, *Spermophilus columbianus* (Betts 1976); the thirteen-lined ground squirrel, *S. tridecemlineatus*, and the spotted ground squirrel, *S. spilosoma* (Streubel 1975); and Belding ground squirrel, *S. belding* (Morton 1975)] illustrate the significant effects exogenous and endogenous factors have on the time allotted to various activities. My objectives were (1) to produce time budgets for the Wyoming ground squirrel, *Spermophilus elegans* (*sensu* Nadler, Hoffmann, and Greer 1971; (2) to document differences in time budgets due to age and sex; (3) to correlate variation in time budget with several environmental factors: weather, day since emergence, hour of day, and presence of predators; and (4) to assess the ecological and evolutionary correlates of these variations in time budget.

METHODS

A colony of free-ranging Wyoming ground squirrels was observed from 18 May 1974 to 24 August 1974 and from 20 April 1975 to 20 August 1975 in a montane meadow (2440 m elevation) in the Front Range of the Rocky Mountains approximately 16 km southwest of Boulder, Colorado (Zegers and Williams 1979).

Using the technique of Wiens et al. (1970), I employed an electronic metronome,

binocular, and a 20X telescope to observe the squirrels from a blind. The animals were marked for individual recognition from a distance using a unique combination of freeze brands (Hadow 1972) located at one or two of the spots on the animal's body.

The behavior of these ground squirrels was divided into 13 categories (i.e., activities) (Zegers 1977). This classification scheme is similar to those previously used for this squirrel (Clark and Denniston 1970) and for the closely related Richardson's ground squirrel, *S. richardsonii* (Quanstrom 1968 and 1971). These 13 activities and their definitions are as follows:

1. The basic posture is a resting and observation position with all four paws on the ground.
2. Semi-alert posture is a resting and observation position in which the forepaws are off the ground and the back is arched.
3. The alert position is a resting and observation position in which the forepaws are off the ground and the back is straight, not arched.
4. The down feeding posture is a variation of the basic posture in which the squirrel is eating. Food is manipulated using the teeth and lips without the aid of the forepaws.
5. The upright feeding posture is a variation of either the semi-alert or alert postures in which food is handled with the forepaws.
6. Running is a rapid locomotor activity in which the animal is moving ≥ 1.0 m/s and is not involved in a chase.
7. Chasing is running in which the individual is chasing another.
8. Chased is running in which the individual is being chased.
9. Walking is relatively slow (compared to running) locomotion of < 1.0 m/s.
10. Hay-gathering involves stuffing herbaceous stems and leaves into the mouth without chewing and

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swallowing. These materials are cut or pulled up by use of the forepaws and teeth and placed in the mouth perpendicular to the sagittal line and then deposited somewhere underground.

11. Grooming includes self- and allogrooming as well as dusting, in which a squirrel rolls from side to side while prostrate in the dirt of an entrance mound.
12. Digging is the behavior in which a squirrel removes soil from a tunnel entrance by using either or both hind limbs and forelimbs.
13. Fighting is similar to fighting among other rodents, and involves rolling, biting, clawing, and yelping.

Other data were collected for each of 1125 observation periods, which lasted from 5 to 15 minutes. These data included date, time of observations, animal identification number, information about predators (i.e., whether or not a predator was visible, and, if so, its species), and weather conditions. Air temperature was measured at 0.5 m above ground every half hour. Sky cover was divided into four cloud categories: clear (no clouds), partly cloudy (less than 50 percent of sky covered), mostly cloudy (more than 50 percent of sky covered) and overcast (complete cloud cover).

Differences in time budget due to age and sex were tested via chi-square analysis. The relationship between five environmental factors and the components of time budget were analyzed by multiple regression. Air temperature, day since emergence, hours of day, sky conditions, and presence of predators served as independent variables, and the frequencies of each of the 13 activities for each of the observation periods were the dependent variables.

RESULTS AND DISCUSSION

Although the behavior of *S. elegans* has been studied (Clark 1970a, Clark and Denniston 1970, Pfeifer 1980), a time budget has never before been constructed. Aboveground time budget for all individuals is shown in Figure 1. Note that the two feeding activities were the most protracted, combining to consume 39.3 percent of all time spent above ground. The three sedentary but watchful positions (basic, semi-alert, and alert) were the next most frequent, followed by the five postures labeled "individual maintenance." Note that the three agonistic activities were the least frequent.

Few time budgets of other sciurids are available for comparison. Betts (1976) found that feeding consumed from 49 to 86 percent, and "alertness" occupied from 6 to 26 percent of the total time above ground of *Spermophilus columbianus*. *Tamiasciurus*, the red squirrel, spent approximately 35 percent of its total time above ground feeding, although this percentage ranged from 9 to 60 percent (Smith 1968). Streubel (1975) found *Spermophilus tridecemlineatus* spent 42.4 percent and *S. spilosoma* spent 45.6 percent of its time feeding, but only 11.6 percent and 15 percent, respectively, in some alert postures. Sexual and agonistic behavior comprised less than 5 percent of the total budget for these species. When above ground, Wyoming ground squirrels spent a smaller proportion of their time feeding, and more time in sedentary observation than these other species. This may be due to a greater threat from predators, or to prevailing habitat conditions resulting in differences in social system or foraging strategy.

These differences in time budget also reflect differences in territorial maintenance strategy. For example, *Tamiasciurus*, a squirrel that defends a food supply, uses a strategy that spends little time on actual territorial defense (0.25 to 1.85 percent of active time, Smith 1968). Complete defense is probably difficult if not impossible in the spatial complexity of the coniferous forest. It appears to be energetically adaptive to use warning calls and to tolerate some intrusion rather than to spend considerable time and energy chasing other squirrels. *Spermophilus spilosoma* and *S. tridecemlineatus* do not defend food supplies. Their territoriality can be described as core monopolization (Streubel 1975), in which individual distance and the tendency to remain near the home burrow spaces individuals. No cooperative or extended familiar behavior and little agonistic behavior occur (Streubel 1975). In contrast, *S. richardsonii* and *S. elegans* do not defend food territories but do defend reproductive territories. During mating individual males occupy territories that contain the home ranges of several females (Yeaton 1972). These are succeeded by female territories during gestation and lactation (Quanstrom 1968, Yeaton 1972). My observation of female territories for *S.*

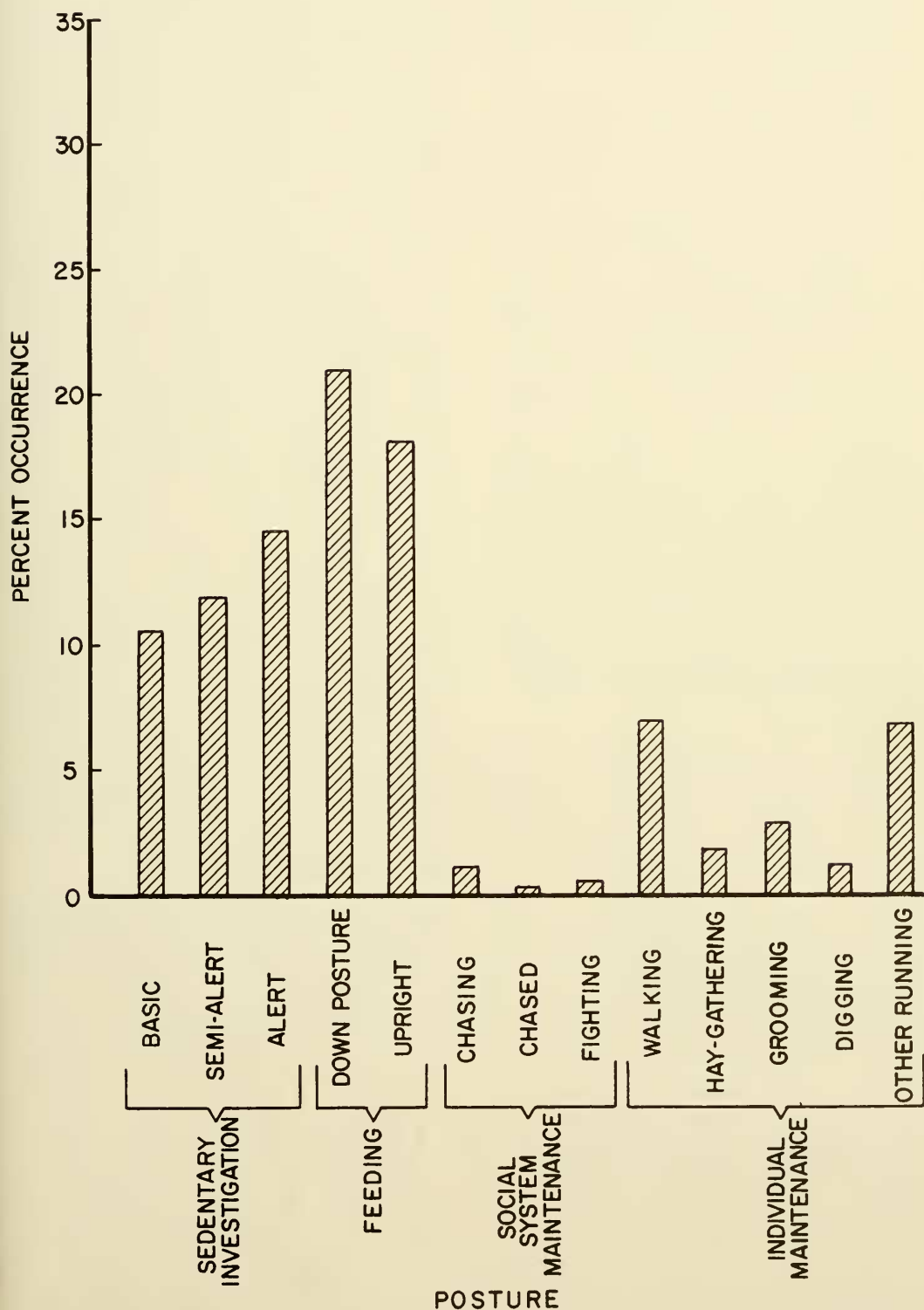


Fig. 1. Time budget of a population of Wyoming ground squirrels during the summers of 1974 and 1975.

elegans revealed them to be essentially used to protect the burrow entrance, (and therefore the young) against intrusion by conspecifics rather than for defending an area of open ground.

The differences in time budget between sexes for adults and between age groups are shown in Figures 2 and 3. Time budgets of adults differed significantly from those of juveniles ($X^2 = 38.67$; $df = 12$; $p < 0.05$) but sex did not have a significant effect on time budget ($X^2 = 0.73$; $df = 12$; $p > 0.05$). The effects of age and sex on time budgets have not been studied extensively for sciurids. I know of only one other study of sciurids that presents time budget data by age and sex groups. Although the data were not statistically analyzed, the time budgets of adult and yearling *S. columbianus* appear to be substantially different from those of juveniles (Betts 1976). Moreover, differences between adults and yearlings and between males and females existed. Likewise, my data indicate a significant difference between age groups, although the difference between sexes was not significant. The apparent time budget differences between sexes of the Columbian ground squirrel suggest that that species has a more pronounced division of labor than *S. elegans*.

Differences in time budget between adults and juveniles are important and obvious. Feeding to support growth is not as important to adults as to juveniles. Adults come out

of hibernation essentially full grown and must only consume sufficient energy to reproduce successfully and to deposit enough fat to survive hibernation. Juveniles, however, grow at a rate of 11.4 percent per day during the first weeks after birth until full length is achieved at about 63 days of age (Clark 1970a). In addition, the juveniles must then put on enough fat to survive hibernation. Moreover, for both *S. richardsonii* and *S. elegans* a temporal difference exists between adults and juveniles in their activities. Adults are finished with aboveground activities before juveniles start prehibernatory fattening (Clark 1970b, Dorrance 1974, Michener 1972 and 1974, Quanstrom 1968, and Zegers 1977). This removes adults from the area when the juveniles are preparing for hibernation and, by reducing intraspecific competition, probably increases survival of juveniles (Yeaton 1969). Likewise, early immergence of adults into hibernacula may increase adult survivorship by reducing predation pressure (Morton 1975).

Several sciurids are known to modify activity periods in response to environmental factors (Yeaton 1969, Clark 1970b, Quanstrom 1971, Baudinette 1972, G. R. Michener 1973). Multiple regression of environmental factors on the 13 components of the time budget of Wyoming ground squirrels revealed some interesting relationships to that budget (Table 1). None of the independent variables correlated with frequency of

TABLE 1. Independent variables which were significant predictors of the frequency of 13 activities of *Spermophilus elegans*. Presence of predator (Pred), hour of day, day since emergence, air temperature, and sky conditions were analyzed for their effect on the frequency of each activity. Direction of the correlation is indicated by the sign (+ or -). n.s. = not significant

Activity	Independent variables ($p < 0.05$ for beta)				
	Pred	Hour	Day	Temp	Cloudiness
Basic	n.s.	+	n.s.	-	n.s.
Semi-alert	+	n.s.	-	-	n.s.
Alert	+	n.s.	n.s.	+	n.s.
Feeding down	-	+	n.s.	-	n.s.
Feeding upright	-	-	+	+	n.s.
Chasing	-	n.s.	+	n.s.	n.s.
Chased	-	n.s.	+	n.s.	-
Other running	-	n.s.	-	n.s.	+
Walking	-	-	-	-	n.s.
Hay gathering	-	-	n.s.	n.s.	n.s.
Grooming	-	n.s.	+	n.s.	n.s.
Digging	-	+	n.s.	-	-
Fighting	n.s.	n.s.	n.s.	n.s.	n.s.

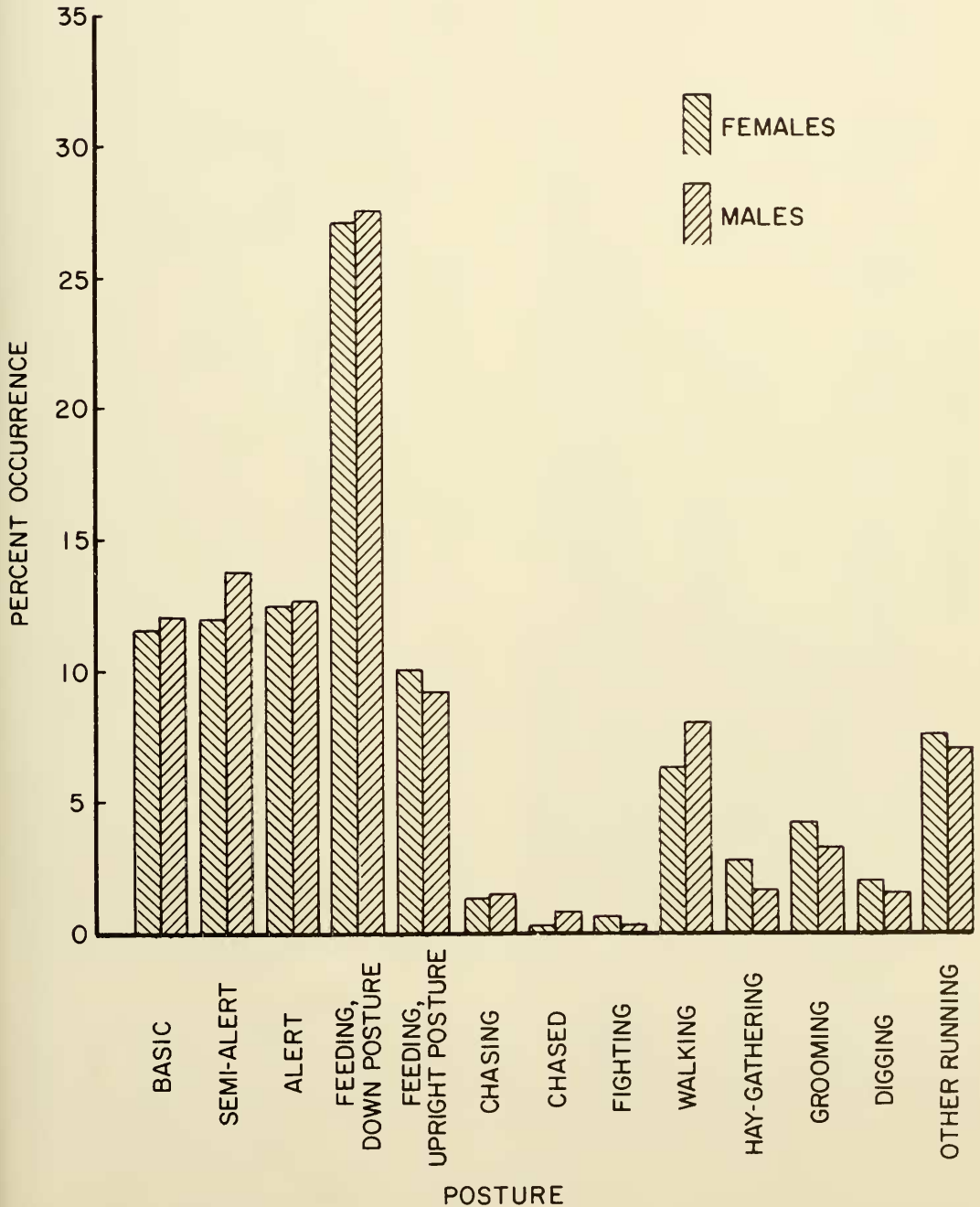


Fig. 2. Comparison of time budgets of adult male and adult female Wyoming ground squirrels during the summers of 1974 and 1975.

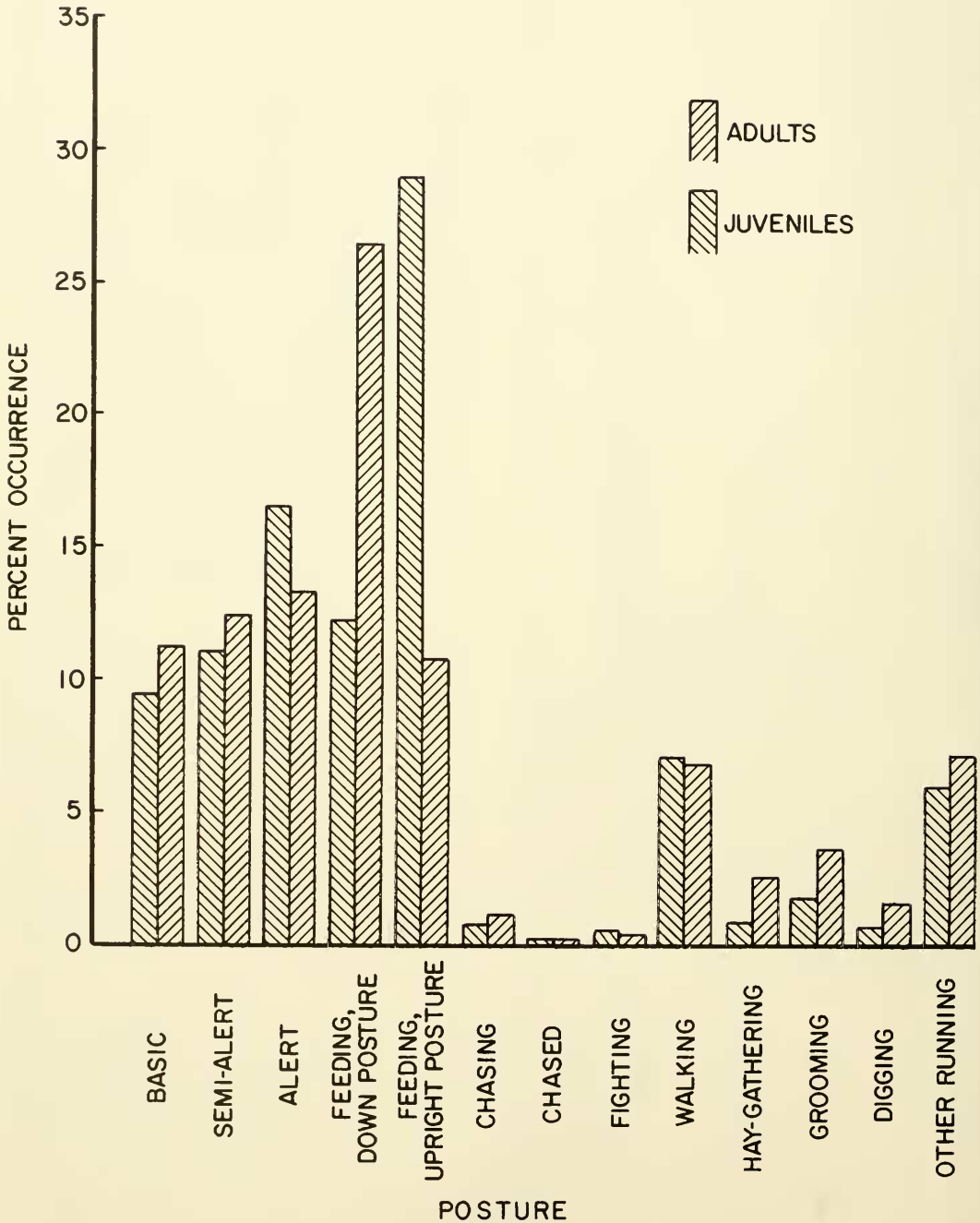


Fig. 3. Comparison of time budgets of all adult and juvenile Wyoming ground squirrels during the summers of 1974 and 1975.

fighting. This reflects the obvious social nature of fighting; social situation was obviously the most important factor in initiating fighting, which went on regardless of the hour, date, or weather.

The presence of a predator was the most recurring significant variable (Table 1), correlating with the frequency of 11 activities. The most casual observer of these squirrels would agree that behavior is greatly modified once a predator is detected by the squirrels. All feeding, social activity, grooming, etc., stopped as the squirrels, using either the basic, semi-alert, or alert postures, intently observed the predator.

Day since emergence correlated with feeding postures, chasing, chased, walking, and grooming activities. This indicates chronological changes in the time budget (Zegers 1977). As the season proceeded, adults became progressively more sedentary and spent less time feeding, although they continued to gain weight (Zegers and Williams 1977). This quiescence could be due to diminished metabolic rate during prehibernatory fattening (Armitage and Schulenberger 1972). In addition, the squirrels might have been able to spend less time feeding and still gain weight because the energy drain of reproduction and territorial defense was no longer present. Regardless of the cause of their quiescence, the alertness of these individuals probably aided in predator detection and thereby contributed to the survival of juveniles. This interpretation is supported by the fact that in the last two weeks before disappearing into hibernacula these adults stopped gaining weight and on the average actually lost weight (Zegers and Williams 1977). Some factor other than insufficient body fat was preventing these adults from hibernating two weeks earlier. Perhaps this factor was parental care.

The effects of ambient temperature, cloud cover, and hour of the day on sciurid time budgets are generally interpreted as thermoregulatory and water balance mechanisms. Michener (1968) demonstrated that *S. richardsonii* modified overall activity in response to air temperature and light intensity (i.e., cloudiness) in ways that promoted overall maintenance of body temperature and water balance. My data show that air temperature

and cloudiness also affect specific behaviors, although this conclusion must be qualified. Many behaviors were not influenced by weather conditions (Table 1). Although running decreased on sunny days, digging increased. As air temperature increased squirrels walked and dug less. This may reflect generally lower activity when temperatures are high. Although this could be a thermoregulatory response, the data in Table 1 generally support the idea that specific behaviors of ground squirrels tend not to be greatly influenced by weather conditions. These squirrels were above ground apparently for a purpose (e.g., feeding, territorial defense, predator detection). If weather conditions were unfavorable enough to seriously interfere with these activities, the animals returned to their burrows. If, however, conditions were less than ideal but not sufficient to force them into burrows, the squirrels may have responded with slight modifications of (1) the frequency of some behaviors or (2) posture. For example, on cold, sunny days the squirrels used postures that maximized their heat gain from the sun, whereas on hot, sunny days they used postures that minimized heat gain from the sun (Zegers 1977). In general, activity level (i.e., number of individuals above ground at any one time) decreased during cool and cloudy periods and during hot and sunny periods. Likewise Baudinette (1972) found that the California ground squirrel, *S. beecheyi*, avoided the warmest periods of summer days by remaining in the favorable environment of the burrow. The blacktail prairie dog, *Cynomys ludovicianus*, (Althen 1975) also showed peak activity above ground synchronous with times of optimal microenvironmental thermal conditions.

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